

## Does wing shape of andromorph females of *Calopteryx splendens* (Harris, 1780) resemble that of males?

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Female limited polymorphism consists in the coexistence of two or more female morphs in the same population and is widespread among odonates. Generally, one female morph, the andromorph, resembles males in colour or, sometimes, also in morphology and behaviour, while one or more other morphs, gynomorphs, differ from males. This phenomenon is probably promoted by advantages to females which arise from reduced sexual harassment. Andromorph females of *Calopteryx splendens* keep wing spots, like males (although these ornaments do not match exactly male wing spot colour), while gynomorphs have hyaline wings. Males and gynomorphs show a marked sexual dimorphism in wing shape, and this determines flight patterns which differ between sexes. If andromorphs mimic male wing spots to avoid harassment, they may also benefit from mimicking the male flight morphology, and consequently the male flight pattern. In this case wing shape of andromorph and gynomorph females would differ, as the wing shape of andromorphs resembles that of males. In this study we compared the wing morphology of males and of the two female morphs of *C. splendens* using geometric morphometrics. Our results revealed that andromorphs and gynomorphs of this species share the same wing shape, size, and static allometry, and this suggests that flight patterns should also be shared by the two morphs. Thus, females might avoid male harassment by mimicking exclusively male wing pigmentation (male mimicry hypothesis), or confound males through an uncommon appearance (learned mate recognition hypothesis).

**Keywords:** Odonata; dragonfly; *Calopteryx*; geometric morphometrics; andromorph; gynomorph; polymorphism

### Introduction

Female limited polymorphism (hereafter FLP; sometimes known as polychromatism; Corbet, 1999) consists in the existence of two or more female morphs in the same population and at the same time (Van Gossum, Sherratt, & Cordero-Rivera, 2008). This phenomenon has been described in many animal taxa, for example birds (Bleiweiss, 1992; Roulin, Ducret, Ravussin, & Altwegg, 2003) and butterflies (Turner, 1978; Clarke, Clarke, Collins, Gill, & Turner 1985; Herrell & Hazel, 1995; Nielsen & Watt, 2000), and is often associated with the occurrence of alternative reproductive strategies, which involve complex combinations of behavioural, morphological, physiological, and life history characteristics (Corbet, 1999; Cordero & Andrés, 1996; Hammers & Van Gossum, 2008; Sherratt, 2001). In odonates, FLP is particularly widespread, both in dragonflies (Corbet, 1999; Prasad, Ramakrishna, Srinivasulu, & Srinivasulu,

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2013) and damselflies (Andrés & Cordero 1999; Andrés & Cordero Rivera 2001; Cordero, 1992; Fincke, 1994; Fincke, Jödicke, Paulson, & Schultz, 2005; Sánchez-Guillén, Van Gossum, & Cordero Rivera, 2005; Sirot, Brockmann, Marnis, & Muschett, 2003; Wong, Smith, & Forbes, 2003). Generally, in odonates one morph, the andromorph, resembles males in body colour (see for example Cordero & Andrés, 1996) or in other additional characters (see for example Bots et al., 2009), while the other(s), the gynomorph(s), do not (or respectively androchromic and gynochromic, if referring only to body colour).

Mechanisms for the evolution and for the maintenance of such polymorphism remain poorly understood, and may not be mutually exclusive. A number of hypotheses have been proposed to explain this phenomenon. For example, the male-mimicry hypothesis, and its variations, suggest that andromorph females are not easily recognized as mates by males, thus avoiding the costs of male harassment and superfluous matings (Cordero, 1992; Cordero, Santolamazza Carbone, & Utzeri, 1998; Hinnekint, 1987; Johnson, 1975; Robertson, 1985; Sherratt, 2001; Van Gossum et al., 2010). On the other hand, it has been hypothesized that the presence of different females morphs, independently of their male mimicry, leads to a negative frequency dependent mechanism in which males develop a mate preference for the most common female morph, reducing harassment on the less frequent morph/s (learned mate recognition [LMR]: Fincke, 2004; Iserbyt, Bots, Van Gossum, & Sherratt, 2013; Miller & Fincke, 1999; Van Gossum, Stoks, Matthysen, Valck, & De Bruyn, 1999; Van Gossum, Stoks, & De Bruyn, 2001b).

Andromorphs may only mimic male colour, but sometimes they possess other male-like characters. For example, andromorphs may react in a male-like way when approached by males and have been observed to fly less distance than gynomorphs (*Ischnura elegans*; Van Gossum, Stoks, & De Bruyn, 2001a), or threaten males more frequently (*I. ramburii*; Sirot et al., 2003). These behavioural differences between morphs might be associated with flight differences (Bots et al., 2009). In fact, in insects wing shape is a very plastic character subjected to natural selection for flight performance optimization (see for example Berwaerts, Van Dyck, & Aerts, 2002; Betts & Wootton, 1988; Wakeling & Ellington, 1997a, 1997b, 1997c) and, in odonates, different wing shapes may be selected according to specific behaviour (Johansson, Söderquist, & Bokma, 2009; Outomuro, Rodríguez-Martínez, Karlsson, & Johansson, 2014; Sacchi & Hardersen, 2012). Consequently, wing morphology could diverge among female morphs, and andromorphs might show more male-like wing shapes (e.g. Abbott & Svensson, 2008; Bots et al., 2009).

Most studies on FLP focused on Coenagrionidae, but this phenomenon occurs also in species belonging to other families, such as Calopterygidae. In the European members of this family, FLP is present in some species of the genus *Calopteryx*. In most European populations of *C. splendens* (Harris, 1780) females are monomorphic, but, in some populations in the southern Balkan and in the Middle East FLP occurs (Buchholtz, 1955; Weekers, De Jonckheere, & Dumont, 2001), while in Italy FLP is restricted to southern regions (De Marchi, 1990).

Males of *C. splendens* have pigmented wings, which are used for intrasexual competition and for mate courtship (Córdoba-Aguilar & Cordero Rivera, 2005). Gynomorph females have hyaline-greenish wings; instead, andromorphs mimic male wing ornaments, but the pseudopterostigma is white as in hyaline winged gynomorphs (De Marchi, 1990). Wing ornaments of andromorphs generally differ in colour from those of males, being brown instead of black-blue (De Marchi, 1990), with the exception of some populations in the Balkan peninsula, where andromorphs have exactly male-like wing colours (Fudakowski, 1930). The genetic and physiological basis of such polymorphism is still unknown. Female wing spots have been hypothesized to have an anti-harassment function towards both conspecific and heterospecific males (Cordero & Andrés, 1996; De Marchi, 1990).

A pronounced sexual dimorphism in wing shape occurs in *C. splendens*, mainly as a consequence of the strong sexual selection for wing pigmentation in males leading to a co-evolution between wing shape and wing pigmentation (Outomuro, Adams, & Johansson,

2013). Consequently, males have shorter and more “rounded” wings, which increase the area available for pigmentation (Outomuro & Johansson, 2011; Outomuro, Bokma, & Johansson, 2012). In contrast, hyaline winged females have longer and more tapered wings, primarily due to natural selection for extensive flights (Betts & Wootton, 1988), and *Calopteryx* females are known to move more than males (Chaput-Bardy, Grégoire, Baguette, Pagano, & Secondi, 2010; Outomuro et al., 2012). Females will benefit from more slender wings, which produce more lift, also because they carry eggs in the abdomen (Outomuro et al., 2012; Wootton, 1992). This difference in shape is also related to sex specific flight patterns: males show reduced flight speed and increased wing beat frequency with respect to females (Hilfert-Rüppell & Rüppell, 2009).

If andromorphs mimic male wing spots to avoid harassment, they may take advantage also of mimicking male flight pattern (Bots et al., 2009). If so, wing shape of andromorphs should differ from that of gynomorphs. Thus, in this work we applied geometric morphometrics techniques to study the wing morphology of males and of the two female morphs of *C. splendens*.

## Materials and methods

### Sampling

We sampled 33 males, 49 andromorph females and 49 gynomorph females of *C. splendens* on 18–21 July 2013 in two sites near Teggiano (southern Italy; Table 1 for coordinates and sampling sizes). We obtained digital images of their wings using a scanner (HP Scanjet G4010, Hewlett-Packard Company, Palo Alto, CA, USA, resolution of 600 DPI). Individuals were scanned dorsally, while the wings were blocked by two pieces of polyurethane foam held down with a weight of about 50 g, including a strip of graph paper to provide a scale (Cigognini, Gallesi, Mobili, Hardersen, & Sacchi, 2014). This system prevented movement, and did not cause any damage to the insect. Individuals were marked prior to release at the site of origin, in order to avoid recapture.

### Geometric morphometrics methods

We quantified wing shape using landmark based geometric morphometrics methods (Adams, Rohlf, & Slice, 2004; Bookstein, 1997; Rohlf & Marcus, 1993). These methods allow for the quantification of shape using generalized procrustes analysis (GPA; Adams et al., 2004; Rohlf & Slice, 1990), which scales, translates and rotates landmark configurations, removing the effect of non-shape variation (Bookstein, 1997; Rohlf & Marcus, 1993). Information about size is retained as centroid size (CS), defined as the square root of the sum of the squared distances between each landmark and the specimen centroid. We defined 10 homologous landmarks, located where main veins met the edge of the wing (Figure 1), both in forewings and hind wings using TpsDig2 software (Rohlf, 2010). Only right wings were considered. Afterwards, we performed a GPA on digitized landmark configurations, obtaining aligned configurations. Information about wing dimensions were retained as logarithm of the centroid size (LogCS), and were used to account for shape variability due to static allometry. Then, we performed a principal components analysis

Table 1. Coordinates of sampling sites and related sampling sizes.

Sampling site coordinates	Andromorphs	Gynomorphs	Males
40°19'13" N, 15°37'22" E	29	30	16
40°22'22" N, 15°33'10" E	20	19	17

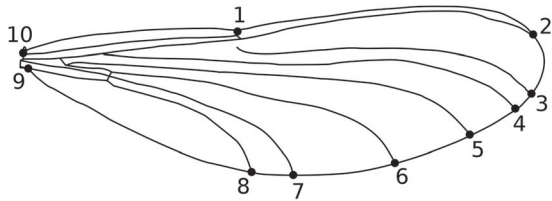


Figure 1. Locations of the 10 landmarks, defined by the intersection of wing margin and: (1) nodus; (2) first radius; (3) third radius; (4) third radius intercalary; (5) fourth + fifth radius; (6) medius; (7) first cubitus; (8) second cubitus; (9) proximal apex of anal triangle; (10) connection costa–subcosta. Nomenclature of veins follows Dumont (1991).

(PCA) on the variance–covariance matrix of the landmark coordinates of the aligned configurations to obtain shape variables (Claude, 2008). Since the dimensionality of the data is  $2 \times p - 4$ , where  $p$  is the number of landmarks (in our case  $2 \times 10 - 4 = 16$ , Dryden & Mardia, 1998), we used the scores of the first 16 principal components (PCs) as a set of shape variables.

Statistical analyses

We studied wing shape variation between morphs and sexes using the set of shape variables as dependent variable in a MANCOVA, including group (andromorph, gynomorph and male), sampling site, individual size (estimated through the wing LogCS) and their interactions as predictors. LogCS was chosen as index of individual body size, since measures of size are strongly correlated (e.g. Outomuro et al., 2013; Outomuro & Johansson, 2011), and was used to control for static allometry of wing shape. Individual size  $\times$  group interaction, if occurring, could reveal differences in static allometry between morphs, that may reflect differences in flight behaviour (Outomuro et al., 2013) between andromorphs and gynomorphs. Finally, size variation among groups was investigated through a factorial ANOVA using wing LogCS as dependent variable and group, sampling site and their interactions as factors. All models in the analysis were performed on both forewings and hind wings, and were simplified by removing non-significant terms (significance threshold:  $\alpha = 0.05$ ) starting from interactions (Zuur, Ieno, Walker, Saveliev, & Smith, 2009). The patterns of shape variation detected by models were visualized using vectors showing displacements between corresponding couples of landmark of two predicted shapes. We used the software R version 3.2.0 (R Development Core Team, 2015) for statistical analyses, and the R package “geomorph” (version 2.1.4, Adams & Otárola-Castillo, 2013) for geometric morphometrics.

Table 2. Minimum significant models obtained from the MANCOVAs performed on shape variables of forewings and hind wings of males as well as andromorphic and gynomorph females.

Model	df	Pillai’s trace	<i>p</i>
Forewing			
Group	2	0.461	0.001
Size (logCS)	1	0.231	0.015
Sampling site	1	0.132	0.41
Hind wing			
Group	2	0.710	< 0.001
Size (logCS)	1	0.243	0.009
Sampling site	1	0.261	0.004

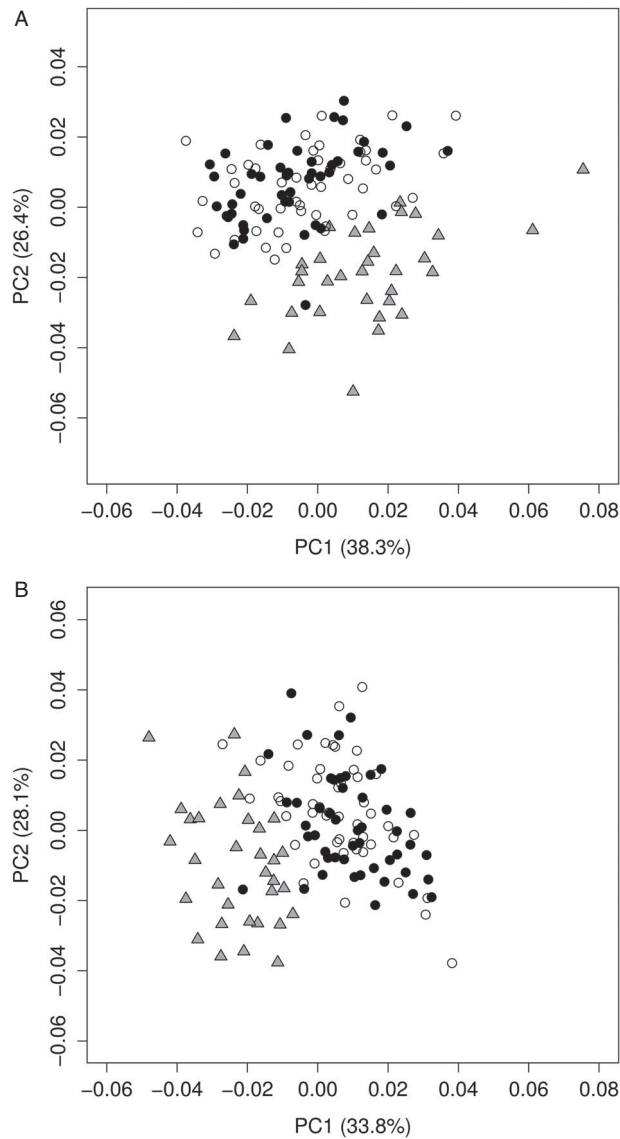


Figure 2. Plot of the first two PCs for (A) forewing and (B) hind wing shapes. Black dots andromorphs; open dots gynomorphs; grey triangles males.

## Results

### Wing shape

The MANCOVA performed on the forewing shape did not produce any significant interaction (Pillai's trace < 0.295,  $p > 0.06$ ), so they were removed. In the final model we retained the statistically significant effects of group and individual size, while sampling site was not significant (see Table 2 for statistics). The shape of male forewings differed markedly from gynomorphic and andromorphic females, but no difference emerged between females morphs (Figures 2A, 3A, 3B). Similar results were obtained from the analysis performed on the hind

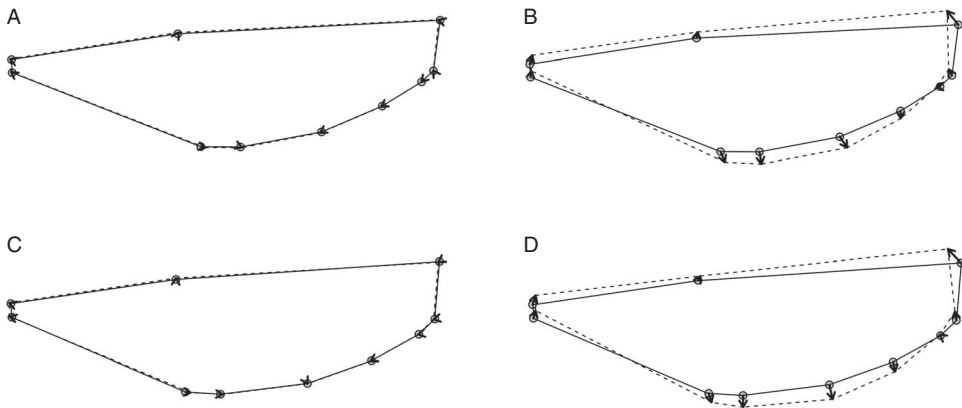


Figure 3. Vector displacements between corresponding landmarks: (A) forewing shape changes from andromorphs (bold) to gynomorphs (slashed); (B) forewing shape changes from andromorphs (bold) to males (dashed); (C) hind wing shape changes from andromorphs (bold) to gynomorphs (slashed); (D) hind wing changes from andromorphs (bold) to males (dashed).

wings: all two-way interactions were dropped (Pillai's trace < 0.336,  $p > 0.11$ ) and the final model retained all three main effects (see Table 2 for statistics). The pattern of shape variability was the same as observed in the analysis for forewings: the shape of the hind wings differed markedly between sexes, but did not differ between female morphs (Figures 2B, 3C, 3D). The absence of size  $\times$  group interaction in both wings revealed that wings of the two female morphs follow the same static allometry pattern.

### Size

The linear model used to study size differences in forewings retained only the main effects of group and sampling site, with only the former statistically significant (group:  $F(2,126) = 177.62$ ,  $p < 0.001$ ; site:  $F(1,126) = 0.95$ ,  $p = 0.33$ ), since the group  $\times$  sampling site interaction was not significant (at removal  $F(2,124) = 0.61$ ,  $p = 0.55$ ). In the same analysis performed on the hind wings the interaction was dropped (at removal  $F(2,124) = 0.66$  and  $p = 0.52$ ). The minimum significant model retained only the effect of group ( $F(2,126) = 129.95$ ,  $p < 0.001$ ) and the non-significant effect of sampling site ( $F(1,126) = 0.04$ ,  $p = 0.85$ ). Males had wings significantly smaller than females (forewing:  $\beta \pm SE = -0.0944 \pm 0.006$ ,  $t(1) = -16.73$ ,  $p < 0.001$ ; hind wing:  $\beta \pm SE = -0.0800 \pm 0.006$ ,  $t(1) = -14.29$ ,  $p < 0.001$ ), but the size of andromorph wings was not significantly different from that of gynomorphs (Figure 4).

### Discussion

In this study we compared wing shape of andromorphic and gynomorphic females and also of males of *C. splendens* using geometric morphometrics. Our specific aim was to investigate differences in wing morphology that can be traced back to different types of flight (Bots et al., 2009). The results of the study did not reveal any difference in shape between wings of the two female morphs. We only found a clear sexual dimorphism between the sexes, irrespective of female morph. Therefore, our data suggest that the two female morphs of *C. splendens* share the same wing morphology. This suggests that also flight dynamics of the two

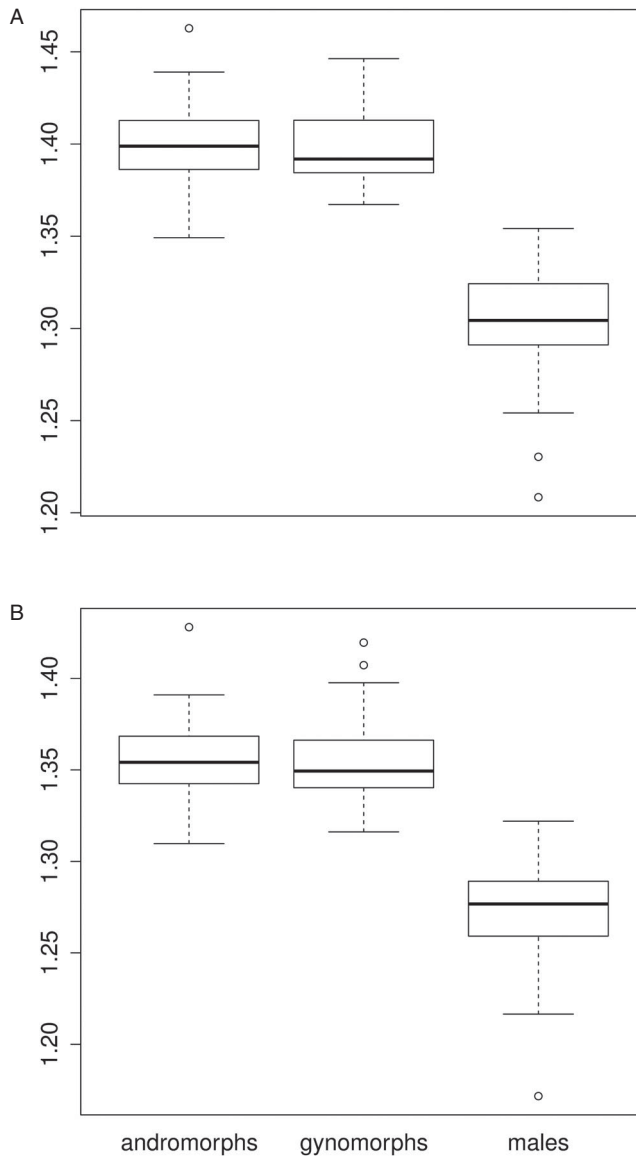


Figure 4. Box plots of (A) forewing and (B) hind wing log transformed CS (centroid size; a measure of size) in andromorphs, gynomorphs and males of *C. splendens*. Box plots illustrate the median (line), the interquartile range of the data (box), and the tails of the distribution ( $1.5 \times$  interquartile range). Circles represent values out of the tails of the distribution.

morphs should be comparable, as this largely depends on wing morphology (Betts & Wootton, 1988).

Interestingly, we did not find any differences in the static allometry of wing shape among female morphs, as revealed by the absence of size  $\times$  morph interaction. Individual size has an important aerodynamic effect on flight performance (Birch, Dickson, & Dickinson, 2004; Sane, 2003), and the lack of differences in allometry between morphs suggests, again, that equally sized females share the same wing morphology and the same flight dynamic, independent of morph. It follows that andromorphs of *C. splendens* should not mimic male flight, and their anti-harassment strategy seems to depend exclusively on pigmented wing spots.



The fact that andromorph females do not mimic male wing morphology and in consequence do not mimic male flight behaviour has a number of implications.

On the one hand, exclusively mimicking male ornaments by females might be enough to reduce harassment, as is probably true for *I. elegans* (*sensu* Cordero Rivera & Sánchez-Guillén, 2007; Hammers & Van Gossum, 2008; Van Gossum et al., 2010; but see Van Gossum, De Bruyn, & Stoks, 2005; Van Gossum et al. 2001a, 2001b). Wing spots in andromorph females of *C. splendens* seem to make females phenotypically more similar to males, and this might be sufficient to reduce mating attempts by conspecific males even though these ornaments do not exactly match male wing spots. This deposition of coloured spots on the wings does not seem to affect flight performance of females. It follows that wing pigmentations of andromorph females is not correlated to wing shape, as has been shown for males (Outomuro et al., 2013; Outomuro & Johansson, 2011). Indeed, male wing morphology in this genus has evolved through strong sexual selection on wing pigmentation leading to a correlation between wing ornamentation and wing shape (Outomuro et al., 2013; Outomuro & Johansson, 2011). Wing shape of males is optimized for manoeuvrability and to optimize the signalling of individual quality during courtship (Outomuro et al., 2013). Generally it is believed that wing shape of females is shaped by natural selection (but see Cigognini et al. 2014), and that females have wings which are slender and long, optimized for extensive flights and lift production (Outomuro et al., 2013). Therefore, mimicking male wing shape could be a fitness cost for andromorph females, and natural selection would favour the typical female wing shape if wing pigmentation alone is sufficient for male-mimicry. Nevertheless, the only other known study that tried to experimentally test this hypothesis (De Marchi, 1990), even if indirectly, found that andromorph *C. splendens* are subjected to reduced harassment, but primarily by other *Calopteryx* males, while *C. splendens* males apparently mate indifferently with the two morphs. So, male ornamentation mimicry of females might be directed towards congeneric *Calopteryx* species, particularly towards *C. haemorrhoidalis*. This explanation may fit in our populations as in our study sites *C. splendens* lives in sympatry with *C. virgo* (very low density), and *C. haemorrhoidalis* (the dominant species). The presence of *C. haemorrhoidalis* males, sharing territories with *C. splendens* males (De Marchi, 1990), might impose enough selective pressure, through excessive harassment and heterospecific mating, to promote selection for andromorph females in *C. splendens*, mimicking males of *Calopteryx* in general. In addition, both intra- and interspecific male mimicry hypotheses are not mutually exclusive, and may cooperate to maintain the FLP in this species. This explanation might also account for the fact that wing pigmentation of andromorph females does not match those of male conspecifics, but is brown (De Marchi, 1990), more similar to that of *C. haemorrhoidalis*. The presence of *C. virgo*, at low density, should induce a comparatively low selective pressure on *C. splendens* females.

The fact that wing spots in andromorphs, in our population, are not exactly like those of males, being smaller and chromatically different from those of males, and the fact that both morphs share the same wing shape, can be interpreted as support for a negative density-dependent model, e.g. LMR (Miller & Fincke, 1999). In this context males are able to create a mate-searching image based on the most abundant female morph, hence andromorphs gain reduced harassment from conspecifics only because they are different from gynomorphs and because they are less frequent, not because of male mimicry. The preference for one or another morph is not innate, but determined by male prior experiences. In this case it is not beneficial for andromorphs to mimic male flight behaviour, because anti-harassment mechanism is based only on the effect of confounding males by the wing colours. Thus, andromorphs should have a wing shape typical of hyaline winged females, being optimized for female specific flight needs. Evidence for LMR in damselflies comes from the genus *Enallagma*, in which males do not show innate preference for gynomorph females, but show learned preference for the morph that they encountered more frequently (Fincke, Fargevielle, & Schultz, 2007).



However, our results are only correlative, and further studies are needed to determine the genetic mechanism that produce female limited polymorphism in this species, as well as field studies on male choice, to determine if such polymorphism in this species is maintained by male mimicry or by a negative frequency dependent model.

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## References

- Abbott, J. K., & Svensson, E. I. (2008). Ontogeny of sexual dimorphism and phenotypic integration in heritable morphs. *Evolutionary Ecology*, 22, 103–121. doi:10.1007/s10682-007-9161-0
- Adams, D. C., & Otárola-Castillo, E. (2013). geomorph: an r package for the collection and analysis of geometric morphometric shape data. *Methods in Ecology and Evolution*, 4, 393–399. doi:10.1111/2041-210X.12035
- Adams, D. C., Rohlf, F. J., & Slice, D. E. (2004). Geometric morphometrics: Ten years of progress following the 'revolution'. *Italian Journal of Zoology*, 71, 5–16. doi:10.1080/11250000409356545
- Andrés, J. A., & Cordero, A. (1999). The inheritance of female colour morphs in the damselfly *Ceriatrion tenellum* (Odonata, Coenagrionidae). *Heredity*, 82, 328–335. doi:10.1038/sj.hdy.6884930
- Andrés, J. A., & Cordero Rivera, A. (2001). Survival rates in a natural population of the damselfly *Ceriatrion tenellum*: effects of sex and female phenotype. *Ecological Entomology*, 26, 341–346. doi:10.1046/j.1365-2311.2001.00338.x
- Berwaerts, K., Van Dyck, H., & Aerts, P. (2002). Does flight morphology relate to flight performance? An experimental test with the butterfly *Pararge aegeria*. *Functional Ecology*, 16, 484–491. doi:10.1046/j.1365-2435.2002.00650.x
- Betts, C. R., & Wootton, R. J. (1988). Wing shape and flight behaviour in butterflies (Lepidoptera: Papilionoidea and Hesperioidea): a preliminary analysis. *Journal of Experimental Biology*, 138, 271–288. Retrieved from <http://jeb.biologists.org/content/138/1/271.short>
- Birch, J. M., Dickinson, W. B., & Dickinson, M. H. (2004). Force production and flow structure of the leading edge vortex on flapping wings at high and low Reynolds numbers. *Journal of Experimental Biology*, 207, 1063–1072. doi:10.1242/jeb.00848
- Bleiweiss, R. (1992). Reversed plumage ontogeny in a female hummingbird: implications for the evolution of iridescent colours and sexual dichromatism. *Biological Journal of the Linnean Society*, 47, 183–195. doi:10.1111/j.1095-8312.1992.tb00664.x
- Bookstein, F. L. (1997). *Morphometric tools for landmark data: Geometry and biology*. Cambridge: Cambridge University Press.
- Bots, J., Breuker, C. J., Van Kerkhove, A., Van Dongen, S., De Bruyn, L., & Van Gossum, H. (2009). Variation in flight morphology in a female polymorphic damselfly: intraspecific, intrasexual, and seasonal differences. *Canadian Journal of Zoology*, 87, 86–94. doi:10.1139/Z08-141
- Buchholtz, C. (1955). Eine vergleichende Ethologie der orientalischen Calopterygiden (Odonata) als Beitrag zu ihrer systematischen Deutung. *Zeitschrift für Tierpsychologie*, 12, 364–386. doi:10.1111/j.1439-0310.1955.tb01533.x
- Chaput-Bardy, A., Grégoire, A., Bague, M., Pagano, A., & Secondi, J. (2010). Condition and phenotype-dependent dispersal in a damselfly, *Calopteryx splendens*. *PLoS ONE*, 5(5), e10694. doi:10.1371/journal.pone.0010694
- Cigognini, R., Galesi, M. M., Mobili, S., Hardersen, S., & Sacchi, R. (2014). Does character displacement demonstrate density-dependent expression in females? A test on the wing shape of two species of European damselflies. *Evolutionary Ecology*, 28, 941–956. doi:10.1007/s10682-014-9711-1
- Clarke, S. C., Clarke, L. F. M. M., Collins, S. C., Gill, A. C. L., & Turner, J. R. G. (1985). Male-like females, mimicry and transvestism in butterflies (Lepidoptera: Papilionidae). *Systematic Entomology*, 10, 257–283. doi:10.1111/j.1365-3113.1985.tb00137.x
- Claude, J. (2008). *Morphometrics with R*. New York: Springer-Verlag.
- Corbet, P. S. (1999). *Dragonflies: Behaviour and ecology of Odonata*. Ithaca: Comstock Publishing Associates.
- Cordero, A. (1992). Density-dependent mating success and colour polymorphism in females of the damselfly *Ischnura graellsii* (Odonata: Coenagrionidae). *Journal of Animal Ecology*, 61, 769–780. doi:10.2307/5630
- Cordero, A., & Andrés, J. A. (1996). Colour polymorphism in odonates: females that mimic males. *Journal of the British Dragonfly Society*, 12, 50–60. Retrieved from [http://ecoevo.uvigo.es/PDF/J\\_Br\\_Dragonfly\\_Soc\\_vol\\_12\\_pp\\_50-60\\_28199629.pdf](http://ecoevo.uvigo.es/PDF/J_Br_Dragonfly_Soc_vol_12_pp_50-60_28199629.pdf)
- Cordero, A., Santolamazza Carbone, S., & Utzeri, C. (1998). Mating opportunities and mating costs are reduced in androchrome female damselflies, *Ischnura elegans* (Odonata). *Animal Behaviour*, 55, 185–197. doi:10.1006/anbe.1997.0603
- Cordero Rivera, A., & Sánchez-Guillén, R. A. (2007). Male-like females of a damselfly are not preferred by males even if they are the majority morph. *Animal Behaviour*, 74, 247–252. doi:10.1016/j.anbehav.2006.06.023

- Córdoba-Aguilar, A., & Cordero-Rivera, A. (2005). Evolution and ecology of Calopterygidae (Zygoptera: Odonata): status of knowledge and research perspectives. *Neotropical Entomology*, 34, 861–879. Retrieved from <http://dx.doi.org/10.1590/S1519-566X2005000600001>
- De Marchi, G. (1990). Precopulatory reproductive isolation and wing colour dimorphism in *Calopteryx splendens* females in southern Italy (Zygoptera: Calopterygidae). *Odonatologica*, 19, 243–250. Retrieved from [http://www.researchgate.net/publication/267459383\\_Precopulatory\\_reproductive\\_isolation\\_and\\_wing\\_colour\\_dimorphism\\_in\\_Calopteryx\\_splendens\\_females\\_in\\_southern\\_Italy\\_28Zygoptera\\_Calopterygidae29](http://www.researchgate.net/publication/267459383_Precopulatory_reproductive_isolation_and_wing_colour_dimorphism_in_Calopteryx_splendens_females_in_southern_Italy_28Zygoptera_Calopterygidae29)
- Dryden, I. L., & Mardia, K. V. (1998). *Statistical shape analysis* (Vol. 4). New York: John Wiley & Sons.
- Dumont, H. J. (1991). *Odonata of the Levant*. Jerusalem: Israel Academy of Sciences and Humanities.
- Fincke, O. M. (1994). Female colour polymorphism in damselflies: failure to reject the null hypothesis. *Animal Behaviour*, 47(6), 1249–1266. doi:10.1006/anbe.1994.1174
- Fincke, O. M. (2004). Polymorphic signals of harassed female odonates and the males that learn them support a novel frequency-dependent model. *Animal Behaviour*, 67(5), 833–845. doi:10.1016/j.anbehav.2003.04.017
- Fincke, O. M., Fargevielle, A., & Schultz, T. D. (2007). Lack of innate preference for morph and species identity in mate-searching Enallagma damselflies. *Behavioral Ecology and Sociobiology*, 61(7), 1121–1131. doi:10.1007/s00265-006-0345-3
- Fincke, O. M., Jödicke, R., Paulson, D. R., & Schultz, T. D. (2005). The evolution and frequency of female color morphs in Holarctic Odonata: why are male-like females typically the minority? *International Journal of Odonatology*, 8(2), 183–212. doi:10.1080/13887890.2005.9748252
- Fudakowski, J. (1930). Über die Formen von *Calopteryx splendens* Harr. aus Dalmatien und Herzegovina (Odonata). *Annales Musei Zoologici Polonici*, 9(6), 57–63.
- Hammers, M., & Van Gossum, H. (2008). Variation in female morph frequencies and mating frequencies: random, frequency-dependent harassment or male mimicry?. *Animal Behaviour*, 76, 1403–1410. doi:10.1016/j.anbehav.2008.06.021
- Herrell, J., & Hazel, W. (1995). Female-limited variability in mimicry in the swallowtail butterfly *Papilio polyxenes* Fabr. *Heredity*, 75, 106–110. doi:10.1038/hdy.1995.110
- Hilfert-Rüppell, D., & Rüppell, G. (2009). Males do not catch up with females in pursuing flight in *Calopteryx splendens* (Odonata: Calopterygidae). *International Journal of Odonatology*, 12, 195–203. doi:10.1080/13887890.2009.9748339
- Hinnekin, B. O. N. (1987). Population dynamics of *Ischnura e. elegans* (Vander Linden) (Insecta: Odonata) with special reference to morphological colour changes, female polymorphism, multiannual cycles and their influence on behaviour. *Hydrobiologia*, 146, 3–31. doi:10.1007/BF00007574
- Iserbyt, A., Bots, J., Van Gossum, H., & Sherratt, T. N. (2013). Negative frequency-dependent selection or alternative reproductive tactics: Maintenance of female polymorphism in natural populations. *BMC Evolutionary Biology*, 13(1), 139. doi:10.1186/1471-2148-13-139
- Johansson, F., Söderquist, M., & Bokma, F. (2009). Insect wing shape evolution: independent effects of migratory and mate guarding flight on dragonfly wings. *Biological Journal of the Linnean Society*, 97, 362–372. doi:10.1111/j.1095-8312.2009.01211.x
- Johnson, C. (1975). Polymorphism and natural selection in Ischnuran damselflies. *Evolutionary Theory*, 1, 81–90. Retrieved from <http://leighvanvalen.com/evolutionary-theory/>
- Miller, M. N., & Fincke, O. M. (1999). Cues for mate recognition and the effect of prior experience on mate recognition in *Enallagma* damselflies. *Journal of Insect Behavior*, 12, 801–814. doi:10.1023/A:1020957110842
- Nielsen, M. G., & Watt, W. B. (2000). Interference competition and sexual selection promote polymorphism in *Colias* (Lepidoptera, Pieridae). *Functional Ecology*, 14, 718–730. doi:10.1046/j.1365-2435.2000.00472.x
- Outomuro, D., Adams, D. C., & Johansson, F. (2013). The evolution of wing shape in ornamented-winged damselflies (Calopterygidae, Odonata). *Evolutionary Biology*, 40, 1–10. doi:10.1007/s11692-012-9214-3
- Outomuro, D., Bokma, F., & Johansson, F. (2012). Hind wing shape evolves faster than front wing shape in *Calopteryx* damselflies. *Evolutionary Biology*, 39, 116–125. doi:10.1007/s11692-011-9145-4
- Outomuro, D., & Johansson, F. (2011). The effects of latitude, body size, and sexual selection on wing shape in a damselfly. *Biological Journal of the Linnean Society*, 102, 263–274. doi:10.1111/j.1095-8312.2010.01591.x
- Outomuro, D., Rodríguez-Martínez, S., Karlsson, A., & Johansson, F. (2014). Male wing shape differs between condition-dependent alternative reproductive tactics in territorial damselflies. *Animal Behaviour*, 91, 1–7. doi:10.1016/j.anbehav.2014.02.018
- Prasad, K. K., Ramakrishna, B., Srinivasulu, C., & Srinivasulu, B. (2013). Odonate diversity of Manjeera Wildlife Sanctuary with notes on female polymorphism of *Neurothemis tullia* (Drury, 1773) (Odonata: Libellulidae) and some species hitherto unreported from Andhra Pradesh, India. *Journal of Entomology and Zoology Studies*, 1(4), 99–104. Retrieved from [http://www.entomoljournal.com/vol1\\_issue4b.html](http://www.entomoljournal.com/vol1_issue4b.html)
- R Development Core Team. (2015). *R: A language and environment for statistical computing*. Vienna: R Foundation for Statistical Computing. Available from <http://www.R-project.org/>
- Robertson, H. M. (1985). Female dimorphism and mating behaviour in a damselfly, *Ischnura ramburi*: females mimicking males. *Animal Behaviour*, 33, 805–809. doi:10.1016/S0003-3472(85)80013-0
- Rohlf, J. F. (2010). tpsDig2 (Version 2. 16) [Software]. Stony Brook: Department of Ecology and Evolution, State University of New York. Available from <http://life.bio.sunysb.edu/morph/>
- Rohlf, J. F., & Marcus, L. F. (1993). A revolution morphometrics. *Trends in Ecology & Evolution*, 8, 129–132. doi:10.1016/0169-5347(93)90024-J

- Rohlf, J. F., & Slice, D. (1990). Extensions of the Procrustes method for the optimal superimposition of landmarks. *Systematic Biology*, 39, 40–59. doi:10.2307/2992207
- Roulin, A., Ducret, B., Ravussin, P.-A., & Altwegg, R. (2003). Female colour polymorphism covaries with reproductive strategies in the tawny owl *Strix aluco*. *Journal of Avian Biology*, 34, 393–401. doi:10.1111/j.0908-8857.2003.03139.x
- Sacchi, R., & Hardersen, S. (2012). Wing length allometry in Odonata: differences between families in relation to migratory behaviour. *Zoomorphology*, 132(1), 23–32. doi:10.1007/s00435-012-0172-1
- Sánchez-Guillén, R. A., Van Gossum, H., & Cordero Rivera, A. (2005). Hybridization and the inheritance of female colour polymorphism in two ischnurid damselflies (Odonata: Coenagrionidae). *Biological Journal of the Linnean Society*, 85, 471–481. doi:10.1111/j.1095-8312.2005.00506.x
- Sane, S. P. (2003). The aerodynamics of insect flight. *The Journal of Experimental Biology*, 206, 4191–4208. doi:10.1242/jeb.00663
- Sherratt, T. N. (2001). The evolution of female-limited polymorphisms in damselflies: a signal detection model. *Ecology Letters*, 4, 22–29. doi:10.1046/j.1461-0248.2001.00184.x
- Sirost, L. K., Brockmann, H. J., Marnis, C., & Muschett, G. (2003). Maintenance of a female-limited polymorphism in *Ischnura ramburi* (Zygoptera: Coenagrionidae). *Animal Behaviour*, 66, 763–775. doi:10.1006/anbe.2003.2279
- Turner, J. R. G. (1978). Why male butterflies are non-mimetic: natural selection, sexual selection, group selection, modification and sieving. *Biological Journal of the Linnean Society*, 10, 385–432. doi:10.1111/j.1095-8312.1978.tb00023.x
- Van Gossum, H., Bots, J., Van Heusden, J., Hammers, M., Huyghe, K., & Morehouse, N. I. (2010). Reflectance spectra and mating patterns support intraspecific mimicry in the colour polymorphic damselfly *Ischnura elegans*. *Evolutionary Ecology*, 25, 139–154. doi:10.1007/s10682-010-9388-z
- Van Gossum, H., De Bruyn, L., & Stoks, R. (2005). Reversible switches between male–male and male–female mating behaviour by male damselflies. *Biology Letters*, 1, 268–270. doi:10.1098/rsbl.2005.0315
- Van Gossum, H., Sherratt, T. N., Cordero Rivera, A. (2008). The evolution of sex-limited colour polymorphism. In A. Córdoba-Aguilar (Ed.), *Dragonflies: Model Organisms for Ecological and Evolutionary Research* (pp. 219–229). Oxford: Oxford University Press.
- Van Gossum, H., Stoks, R., & De Bruyn, L. (2001a). Frequency-dependent male mate harassment and intra-specific variation in its avoidance by females of the damselfly *Ischnura elegans*. *Behavioral Ecology and Sociobiology*, 51(1), 69–75. doi:10.1007/s002650100418
- Van Gossum, H., Stoks, R., & De Bruyn, L. (2001b). Reversible frequency-dependent switches in male mate choice. *Proceedings of the Royal Society B: Biological Sciences*, 268(1462), 83–85. doi:10.1098/rspb.2000.1333
- Van Gossum, H., Stoks, R., Matthysen, E., Valck, F., & De Bruyn, L. (1999). Male choice for female colour morphs in *Ischnura elegans* (Odonata, Coenagrionidae): Testing the hypotheses. *Animal Behaviour*, 57(6), 1229–1232. doi:10.1006/anbe.1999.1100
- Wakeling, J. M., & Ellington, C. P. (1997a). Dragonfly flight. I. Gliding flight and steady-state aerodynamic forces. *Journal of Experimental Biology*, 200, 543–556. Retrieved from <http://jeb.biologists.org/content/200/3/543.short>
- Wakeling, J. M., & Ellington, C. P. (1997b). Dragonfly flight. II. Velocities, accelerations and kinematics of flapping flight. *Journal of Experimental Biology*, 200, 557–582. Retrieved from <http://jeb.biologists.org/content/200/3/557.short>
- Wakeling, J. M., & Ellington, C. P. (1997c). Dragonfly flight. III. Lift and power requirements. *Journal of Experimental Biology*, 200(3), 583–600. Retrieved from <http://jeb.biologists.org/content/200/3/583.short>
- Weekers, P. H. H., De Jonckheere, J. F., & Dumont, H. J. (2001). Phylogenetic relationships inferred from ribosomal ITS sequences and biogeographic patterns in representatives of the genus *Calopteryx* (Insecta: Odonata) of the West Mediterranean and adjacent West European Zone. *Molecular Phylogenetics and Evolution*, 20, 89–99. doi:10.1006/mpev.2001.0947
- Wong, A., Smith, M. L., & Forbes, M. R. (2003). Differentiation between subpopulations of a polychromatic damselfly with respect to morph frequencies, but not neutral genetic markers. *Molecular Ecology*, 12(12), 3505–3513. doi:10.1046/j.1365-294X.2003.02002.x
- Wootton, R. J. (1992). Functional morphology of insect wings. *Annual Review of Entomology*, 37, 113–140. doi:10.1146/annurev.en.37.010192.000553
- Zuur, A., Ieno, E. N., Walker, N., Saveliev, A. A., & Smith, G. M. (2009). *Mixed effects models and extensions in ecology with R*. New York: Springer-Verlag.